Morphological Adaptations to Drought and Reproductive Strategy of the Moss *Syntrichia caninervis* in the Gurbantunggut Desert, China

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Morphological Adaptations to Drought and Reproductive Strategy of the Moss *Syntrichia caninervis* in the Gurbantunggut Desert, China

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The biological soil crusts (BSCs) in the Gurbantunggut Desert, the largest fixed and semi-fixed desert in China, feature moss-dominated BSCs, which play an indispensable role in sand fixation. *Syntrichia caninervis* Mitt. (*S. caninervis*) serves as one of the most common species in BSCs in the desert. In this study we examined the morphological structure of *S. caninervis* from leafy gametophyte to protonema using light and scanning electron microscopy (SEM). We also examined the relationships between the morphological structure of *S. caninervis* and environmental factors. We found that: (1) this moss species is commonly tufted on the sand surface, and its leaves are folded upwards and twisted around the stem under dry conditions; (2) the cells on both upper and lower leaf surfaces have C-shaped dark papillae, which may reflect sunlight to reduce the damage from high temperature; (3) the leaf costa

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is excurrent, forming an awn with forked teeth; and (4) the protonema cells are small and thickset with thick cell walls and the cytoplasm is highly concentrated with a small vacuole. In addition, we also found that the protonema cells always form pouches on the tip of the mother cells during the process of cell polarization. Our results suggest that S. caninervis has, through its life cycle, several morphological and structural characteristics to adapt to dry environmental conditions. These morphological features of S. caninervis may also be found in other deserts in the world due to the world-wide distribution of the species.

Keywords adaptation, morphological structure, protonema development, reproductive strategy, Syntrichia caninervis Mitt.

In arid and semi-arid landscapes, the interspaces between the sparse vegetation are generally covered by communities of highly specialized drought and dehydration tolerant organisms (Hawkes and Flechtner, 2002; Belnap and Lange, 2003; Zhang et al., 2009; Wu et al., 2010). These organisms mainly include cyanobacteria, bacteria, algae, lichens, and mosses, which can form intimate associations with surface soil (Durrell and Shields, 1961; Belnap and Gillette, 1998; Zhang et al., 2009). Generally speaking, biological soil crusts (BSCs) can mainly be classified into three different types including algal crust, lichen crust, and moss crust (Zhao et al., 2009; Zheng et al., 2009). Previous studies have demonstrated that BSCs are an important element of arid ecosystems (Booth, 1941; Belnap and Gillette, 1997; Maestre et al., 2002; Zhang et al., 2006; Zheng et al., 2009; Eldridge et al., 2010), covering up to 70% of the dry land ground surfaces while contributing to soil stability and fertility (Jordan et al., 1978; Maestre et al., 2002; Eldridge and Leys, 2003; Zhang et al., 2002a; Zhao et al., 2009; Wu et al., 2010).

Desert mosses are an essential component of the BSCs in arid regions throughout the world (Eldridge and Bradstock, 1994; Belnap and Lange, 2001; Maestre et al., 2002; Catford et al., 2007; Zheng et al., 2009; Singh et al., 2009; Cole et al., 2010). Like algae and lichens, the mosses in BSCs synthesize carbohydrates via photosynthesis (Stark et al., 2005a; Belnap et al., 2008). Furthermore, desert mosses contribute to sand stability and accelerate vegetation succession (Stark et al., 2007; Dong et al., 2009). In addition, mosses can promote infiltration and retain water in the soil longer, which is an important function for surviving in arid environments (Maestre et al., 2002; Eldridge et al., 2010). Globally, mosses are typically restricted to humid environments, but some mosses, such as the species in the families of Pottiacea, Grimmiacea, and Bryaceae, can survive on the sand surface in arid landscapes (Wang et al., 1999; Wang, 2002; Zhang et al., 2002a; Tian et al., 2005; Xu et al., 2008; Zheng et al., 2009). Desert mosses are extremely sensitive to water shortage and in the absence of water the mosses become dormant, ceasing metabolic processes and photosynthesis (Stepigova et al., 2007; Gao et al., 2009; Xu et al., 2009a). Water is also vital in the sexual reproduction of these mosses, and as it is the only vector for sperm, male and female individuals must be near one another spatially to sexually reproduce (Wyatt, 1977). In arid environments, the limitation of external water dramatically limits the frequency of sexual reproduction in dioecious mosses and population growth is typically accomplished through asexual reproduction (Wu, 1963; Hu, 1985; Stark et al., 1998, 2005b; Menand et al., 2007; Li et al., 2008).

The protonema development in the life cycle of mosses is a unique stage that is not present in other groups of plants except for some liverworts (Nishida, 1978;
Zhao et al., 2002; Li et al., 2006). Because of this unique step, many previous studies on spore germination and protonema development of mosses have been conducted in many parts of the world. Hedwig (1782) first reported the protonema morphology and development of some moss species in Germany. Nishida (1978) investigated the spore germination and protonema development processes of 121 moss species in Japan and described the protonema development process of the moss species. Zhao et al. (2002) studied the spore germination and protonema development of 10 moss species in China.

*Syntrichia caninervis* Mitt. (*S. caninervis*) is a widespread moss species in the BSCs in the Gurbantunggut Desert (Zhang et al., 2002a; Zheng et al., 2009), the largest fixed and semi-fixed desert in northwestern China (Zhang et al., 2002b; Zhang et al., 2009) (Figure 1). In recent years, desert mosses have attracted considerable attention (Wang, 2002; Tian et al., 2005; Stark et al., 2007; Li et al., 2008; Zheng et al., 2009), especially the typical desert moss *S. caninervis* (Stark et al., 2005a; Xu et al., 2008; Xu et al., 2009b; Cole et al., 2010), due to its importance to the desert ecosystem, survival in such a dry hostile environment, and recovery after dehydration. Most studies on *S. caninervis* in arid environments have focused primarily on reproductive biology (Stark et al., 1998; Bowker et al., 2000; Stark et al., 2001, 2004, 2005b), physiology (Stark and McLetchie, 2006; Xu, Liu, et al., 2009), biochemistry (Xu et al., 2009a), and desert recovery abilities (Xu et al., 2008, Cole et al., 2010). Stark et al. (2004) examined the sex-specific rates of leaf regeneration through cultivation of *S. caninervis* and also surveyed the effects of abiotic stressors, such as desiccation, on leaf regeneration. Cole et al. (2010) tested the transplant survivorship of *S. caninervis* in the Mojave Desert. In a laboratory study, Stark et al. (2009) evaluated the upper thermal tolerance and gender specific differences of

![Figure 1](image.png)

Figure 1. (a) The appearance of the Gurbantunggut Desert and biological soil crusts; (b) *S. caninervis*-dominated moss crust; and (c) Shoots of the *S. caninervis*. 
S. caninervis. Xu et al. (2009b) assessed the role of drought by monitoring the physiological responses and asexual reproduction of S. caninervis collected from the Gurbantunggut Desert in China. To our knowledge, however, few studies have attempted to examine the morphological adaptations and reproductive strategies that allow S. caninervis to be successful in drought conditions. In this study we examine: (1) adaptations of the S. caninervis to dry environments; (2) characteristics of protonema development and its adaptation to drought of the S. caninervis; and (3) asexual reproduction strategy of the S. caninervis.

Materials and Methods

Study Area

The Gurbantunggut Desert with an area of $4.88 \times 10^5$ km$^2$, is located in the center of the Jungger Basin ($44^\circ 11' - 46^\circ 20' \text{ N, } 84^\circ 31' - 90^\circ 00' \text{ E}$), Xinjiang Uygur Autonomous Region of China (Figure 2). The climate is typical of cold desert with annual precipitation of 79.5 mm, annual pan evaporation of 2606.6 mm, average temperature 7.26°C, annual mean active accumulated temperature ($\geq 10^\circ \text{C}$) 3000–3500°C and average wind speed of 11.2 m s$^{-1}$ (Wu et al., 2010). Average relative humidity is 50–60%, but it is usually lower than 45% from May to August (Zhang et al., 2009). The study area has sparse vegetation with coverage of $<30\%$ and dominant species of Haloxylon ammodendron and H. persicum. Three types of BSCs (with a thickness of approximately 5 cm) are found in the areas where vascular plants are absent (Figure 1). The stable, fine-textured soil (mainly clay and silt) trapped as dust by the BSCs amount to approximately 15% with a depth of approximately 10 cm. The soil is alkaline (pH values varied from 8.43 to 8.66) and the average content of CO$_3^{2-}$ is 0.0005%, HCO$_3^-$ is 0.0145%, SO$_4^{2-}$ is 0.0025%, Cl$^-$ is 0.002%, Ca$^{2+}$ is 0.0045%, Na$^+$ is 0.001%, Mg$^{2+}$ is 0.001%, and K$^+$ is 0.0025% (Wu et al., 2010).

Field Sampling

Desert moss samples were collected from the sampling site ($44^\circ 35' \text{ N, } 88^\circ 14' \text{ E}$, with an elevation of 447 m and a slope of approximately 35°) in September of 2007, which

Figure 2. Location of the Gurbantunggut Desert and the sampling site.
is located in the southeast portion of the Gurbantunggut Desert (Figure 2). The soil surface was moistened prior to sampling to protect the structure of the BSCs. We used a sterile spatula with a diameter of 8 cm to collect moss samples on the soil surface. Moss samples were collected from three 5 × 5-m permanent plots, mainly based on visual observation of moss crusts and then stored in sterilized plastic bags. Samples were transferred to the laboratory within two days, air dried, and stored at 6–10°C. We identified the moss samples with a microscope (DP70, Olympus Corp, Japan) in the laboratory and selected forty intact *S. caninervis* shoots for further morphological observation and protonema incubation. The height and weight of each selected shoot is approximately 20 mm and 0.001 g, respectively. We then randomly divided the forty *S. caninervis* samples into two subsamples—one for morphological observation (n = 20) and the other for protonema incubation (n = 20).

**Microscopic Analysis**

We examined the *S. caninervis* community characteristics with a stereo microscope (K-500 L, Motic Corp, China). We randomly chose ten intact shoots and dipped them into water for approximately 30 minutes. We then cut each of the mosses into slices by hand with a thickness of approximately 0.03 mm. Finally, we examined the structural characteristics and photographed the mosses with an Olympus BX52 digital microscope (DP70, Olympus Corp, Japan). In addition, three of the samples were freeze-dried overnight and coated with gold for examining finer morphological structures of the species with an S-570 Scanning Electron Microscope (SEM, HITACH Corp, Japan).

**Protonema Incubation**

In order to study the protonema development process, we used the incubation method described by Li et al. (2005). We prepared the Knop solid culture medium with 2% agar but no sugar (Li et al., 2005). We rinsed the mosses with distilled water and dipped them into a 75% alcohol solution for one minute, and then washed them with sterile water. The aforementioned procedures were repeated three times to ensure complete sterilization. Then, we cut the mosses into fragments with a sterilized cutter in a laminar flow cabinet and added 20 mL distilled water to make a moss suspension. We transferred 2 mL of the suspension to the culture medium which was further cultivated under a temperature of 22°C, 60% relative humidity, and 50 μE · m⁻² · s⁻¹ light intensity (Zhao et al., 2002; Li et al., 2005; Stark et al., 2009). During the cultivation we observed daily and noted the development of the protonema in the laboratory conditions with an Olympus BX52 digital microscope (DP70, Olympus Corp, Japan).

**Results**

**Morphological and Structural Characteristics of *S. caninervis***

Microscopic examination revealed that the mosses tufted densely with white awns covering the tops of the stems (Figure 1b, Figure 3g). Further examination of the internal structure through a light microscope revealed that stem cortical cells were large and their walls were obviously incrassated (Figure 3d). Each moss leaf featured an awn with forked teeth at its tip (Figure 3f–3i) and the leaves exhibited a folding and twisting pattern around the stem in drought conditions. The cells on both upper
and lower leaf surfaces had C-shaped dark papillae (Figure 3a–3e). The costa had two large cells in the center to transport water (Figure 3h). As revealed by the Scanning Electron Microscope (SEM), the backside of the *S. caninervis* leaves were coated with several tailpieces such as scutella and squama (Figure 4a); the ventral cells were covered by many branched papillae composed of four or five divarication (Figure 4b–4d); the awn was about 1.2 mm long and covered with a waxy layer (Figure 4e); and the epidermal cells around the leaf costa featured thicker cell walls than the interior cells as shown by the leaf cross-section scans (Figure 4f–4i).

![Figure 3. Morphological structures of *S. caninervis*: a) Upper cells of leaves; b) Lower cells of the moss leaves; c) Upper cross-section of the moss leaves; d) Stem cross-section; e) C-shaped papillae on the cells of leaves (Arrow indicates the C-shaped papillae); f) Costa; g) Awn (Arrow indicates the forked teeth); and h-i) Leaf cross-section (The rectangular indicates the cells that transport water).](image)

**Protonema Developmental Characteristics of *S. caninervis***

The protonema development process of the *S. caninervis* can be divided into three phases: the chloronema cell formation, the protonema growth and leafy gametophyte formation. The chloronema cells were formed from leaf costa and rhizoid and extended to filaments quickly, usually in less than one day (Figure 5c). During the process, the wall of the epidermal cells started bulging to form many pouches.
outside the cell wall in the first day of incubation and then chloroplasts began moving into the pouches from the inner parts of the cell (Figure 5a–5b). Subsequently, the chloroplasts in the chloronema cells started changing from circular to spindly with their numbers decreasing sharply. Meanwhile, the protonema developed from chloronema to caulonema within two days. Five days after the inoculation, the protonema reached 80–100 $\mu$m in length and the first ramification initiated from the base cells (Figure 5d) with the protonema cells changing from columniform to moniliform (Figure 5e). Eight days after the incubation the protonema further elongated to 120 $\mu$m in length and the ramifications also grew longer. At this stage, the protonema started developing the second ramification and formed short branches (Figure 5f–5g). During the process of cell division, the mother cell first expanded at the tip of the ramification to form a pouch and then the cytoplasm flowed into the pouch to create a new protonema cell (Figure 5h–5i). Eighteen days since the initiation of the inoculation, the caulonema and some short branches started

![Figure 4. Structural observations of *S. caninervis* with Scanning Electron Microscope: a) Appearance of the undersurface (Arrow a indicates cuticle ornamentation and arrow b indicates squama); b and c) Papillae on the leaf surface (Arrow indicates papillae); d) Spinous teeth on the costa (Arrow indicates spinous teeth); e) Awn and awn integuments; and f, g, h, and i) Structures of the leaf in cross-section (The rectangular indicates the cells that transport water).](image-url)
changing their colors from green to brown (Figure 5j). At this point, the caulonema had matured, and was ready for the reproduction of gametophytes. Thirty days after the inoculation, the protonema began specialization with some organs developing to rhizoids and others to buds (Figure 5k–5m). Finally, the buds developed to gametophytes with three to six leaves after thirty-six-days of the inoculation (Figure 5n–5o).

Discussion

The protonema development of mosses has been studied for almost one hundred years (Weier, 1933). However, to our knowledge, few studies have been reported on this subject for desert mosses, especially in northwestern China. The studies
examining the relationship between protonema characteristics and environmental factors are also sparse in the literature. Nishida (1973) examined the protonema formation of *Drummondia sinensis* of the Orthotrichaceae in Japan and concluded that the morphological display of short branches is an ecological adaptation to drought environments. Fan (2004) investigated the protonema development processes of 161 moss species in China and found that the 20 species collected in an arid environment in north China had protonema characterized by short branches. Conversely, he found that 45 moss species living in wet environments displayed much longer branches on the protonema. Short branches, usually consisting of 3–6 moniliformis cells with thick walls, have a small surface area to volume ratio and conserve water by reducing water loss through transpiration, indicating an adaptive strategy of the mosses to the dry environment. Fan (2004) has also attributed these characteristics to the adaptation of these species to drought conditions. In the current study, we also found that the protonema of *S. caninervis* has similar short branches, suggesting this species might have adapted to the desert environment morphologically and ecologically.

It is commonly believed that mosses living in humid environments reproduce sexually via spore germination (Nishida, 1978; Gao and Zhang, 1986; Zhao et al., 2002; Fan, 2004; Li et al., 2005, 2006) and asexually in dry conditions (Newton and Mishler, 1994; Stark et al., 2000; Nie et al., 2005). However, we regenerated new moss shoots utilizing gametophyte fragments in humid environments in a laboratory experiment, demonstrating that mosses could use both sexual and asexual reproduction strategies in favorable environments. In the current study, we also found that the asexual reproduction of *S. caninervis* can also start with the protonema which initially breaks into two parts, with each part further developing to a new protonema. This phenomenon may be a unique reproductive strategy for *S. caninervis* in the Gurbantunggut Desert and need to be further confirmed in other desert areas in China and beyond. Previous studies focused on asexual reproduction of desert mosses, including the current study, are mainly laboratory-based experiments with samples collected in the field (Stark et al., 2004; Stark and McLetchie, 2006; Xu et al., 2008; Cole et al., 2010). Direct observations of asexual reproduction stage, to our knowledge, have not been reported in the literature because both sexual and asexual reproduction can produce protonemata that only live a couple of weeks in deserts.

Desert moss *S. caninervis*, a dominant species in BSCs in the Gurbantunggut Desert (Zhang et al., 2002a; Xu et al., 2008; Zhao et al., 2009), is pivotal in maintaining the desert ecosystem functions (Zhang et al., 2002b; Tian et al., 2005; Zheng et al., 2009). Therefore, successfully regenerating such keystone species in field is valuable for the stabilization and restoration of BSC ecosystem in arid and semi-arid lands. Our results that gametophyte fragments of *S. caninervis* can be used for rapid reproduction could be further developed for massive production of this keystone species for restoring the BSCs in degraded desert ecosystems in Northwestern China. In addition, *S. caninervis* is a widely distributed species throughout the world (Stark et al., 2004; Cole et al., 2010). Therefore, our findings could also be extended to other deserts beyond China for ecosystem restoration and management.

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